# Cretaceous anuran and dinosaur footprints from the Patuxent Formation of Virginia

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Abstract.—Footprints of an anuran (gen. et sp. indet.), a theropod dinosaur (*Megalosauropus* sp.), and an ornithopod dinosaur (*Amblydactylus* sp.) have been recovered from the Lower Cretaceous Patuxent Formation in Stafford County, Virginia. These footprints are the first record of terrestrial vertebrates from Cretaceous strata in Virginia, and their discovery suggests that the scarcity of bones and teeth in the Patuxent probably is an artifact of preservation. The anuran trackway provides the oldest known direct evidence for hopping locomotion among these amphibians.

The Patuxent Formation has yielded an abundant fossil macroflora from Maryland and Virginia (Fontaine 1889; Ward et al. 1905; Berry 1908, 1910a, 1910b, 1910c, 1911a, 1911b, 1911c, 1911d; Clark & Miller 1912; Brenner 1967; Wolfe 1972; Doyle & Hickey 1975; Skog 1982, 1988, 1992; Hickey 1986), as well as a diverse palynoflora (Brenner 1963, Hughes & Moody 1966, Doyle 1977, Doyle & Robbins 1977). In sharp contrast, the only vertebrate material reported from this unit is a fish skeleton, found somewhere in the James River valley of Virginia (Berry 1911a). Therefore, it is significant that footprints of an anuran and two kinds of dinosaur have been found north of Fredericksburg, Virginia, in Stafford County (Fig. 1). These prints provide our first glimpse of the Cretaceous vertebrate fauna that once existed in Virginia. The Lower Cretaceous Arundel Formation, which overlies the Patuxent Formation in Maryland but not in Virginia (Fig. 2), has produced a diverse but fragmentary vertebrate fauna that includes turtles, crocodiles, and dinosaurs (Lull 1911a, 1911b; Gilmore 1921; Ostrom 1970; Galton & Jensen 1979; Kranz 1989; Weishampel 1990; Martin & Brett-Surman 1992). The diversity of this fauna suggests that a diverse fauna also

may have existed while the slightly older Patuxent sediments were accumulating. Until the discovery of the footprints described here, however, no direct evidence for such a fauna was available.

Location, age, and geologic setting.-The footprints described here were found by Jon Bachman in strata of the Lower Cretaceous Patuxent Formation in a roadcut on the east side of U.S. Route 1, located 0.25 mi south of Potomac Creek in Stafford County, Virginia (Fig. 1). In its outcrop belt, the Patuxent Formation is approximately 200 to 300 ft thick (Clark & Miller 1912). The unit dips gently and thickens to the east, becoming about 575 ft thick twenty-five mi east-southeast of Fredericksburg, near Oak Grove (Reinhardt et al. 1980). In the Fredericksburg region, pre-Mesozoic crystalline rocks directly underlie the Patuxent Formation with profound unconformity. These rocks crop out along the floor of Potomac Creek well to the west of U.S. Route 1. Because the footprint-bearing outcrop is located toward the eastern margin of the Patuxent outcrop belt, the footprints probably come from the upper half of that formation. However, faults are known from the general vicinity of the footprint-bearing outcrop (Mixon & Newell 1977), so the



Fig. 1. Map showing Bachman locality (star) where footprints have been found in the Lower Cretaceous Patuxent Formation north of Fredericksburg, Virginia (oblique rule). Outcrop belt of Lower Cretaceous Patuxent Formation is shown in dark gray. Younger Tertiary and Quaternary sediments crop out to the east of this belt, while older, pre-Mesozoic igneous and metamorphic rocks crop out to the west (both areas shown in light gray). The Lower Cretaceous strata dip gently toward the east and thicken in that direction.

PERIOD	AGE (Ma)	STAGE	MARYLAND	VIRGINIA	TEXAS	COLORADO / WYOMING	BRITISH COLUMBIA
LOWER RETACEOUS	97.5 113 119	ALBIAN	PATAPSCO FM. ARUNDEL FM.	PATAPSCO FM.	GLEN ROSE FM.	DAKOTA FM	GETHING FM.
		APTIAN BARREMIAN	PATUXENT FM.	PATUXENT FM.	LOWER TRINITY GROUP		CADOMIN FM.
	124	HAUTERIVIAN					
U U	138 144	BERRIASIAN					MINNES FM. MYST MTN. FM.

Fig. 2. Comparison of the Lower Cretaceous geologic columns preserved in Maryland, Virginia, Texas, Colorado/Wyoming, and British Columbia. Time intervals represented by preserved strata are shown; missing time intervals are indicated by gray areas.

stratigraphic position of this outcrop could be lower than it appears to be.

The Patuxent, based on palynomorph studies (Brenner 1963, Doyle & Robbins 1977, Reinhardt et al. 1980), is Barremian to Aptian (124 to 115 Ma) in age. The relatively high horizon of the footprint-bearing bed suggests that an Aptian age (119 to 115 Ma) is more likely than Barremian. The Aptian part of the Patuxent represents a portion of the Lower Cretaceous column that is sporadically but widely preserved in North America (Fig. 2). Thus, a number of Aptian units (the Arundel Formation of Maryland, the Glen Rose Formation of Texas, the basal Dakota Formation of Colorado and Wyoming, and the Cadomin and basal Gething Formations of British Columbia) are close in age to the Patuxent, and their footprints and skeletal remains are especially relevant for comparison to the Patuxent footprints described here.

In its outcrop belt, the Patuxent Formation has yielded only terrestrial fossil remains (Clark & Miller 1912, Berry 1911a), and its sedimentary fabric indicates that most of the unit accumulated in a fluvial braided-stream environment (Glaser 1969). However, about thirty miles east-southeast of the Bachman locality near Oak Grove, glauconite has been reported in the Patuxent in its subcrop belt. Because glauconite forms under marine conditions, the presence of this mineral indicates that marine incursions across the Coastal Plain from the east came within thirty miles of the footprint-bearing locality during Patuxent time (Reinhardt et al., 1980). These regional stratigraphic relationships indicate that the depositional environment of the Patuxent shifted southeastward from fluvial braidedstream through delta plain to marginal-marine delta front environments (Reinhardt et al. 1980). Although the footprint-bearing part of the Bachman locality is dominated by fine-grained sediments (see Table 1), other outcrops in the immediate vicinity tend to be dominated by cross-bedded to massive medium- to coarse-grained sands and sandstones that often are pebbly. This local association of lithologies indicates that the strata at the Bachman locality were formed either in a temporary slack-water area within the lower reaches of a fluvial braided-stream system, or else it was part of a deltaic environment that was briefly established across the lower reaches of a fluvial braided-stream system while its gradient was lowered due to a marine incursion from the east.

The frog footprints were impressed on a clayey silt layer that dried out enough not to be disrupted by deposition of an inchthick (2.5 cm-thick) layer of ripple-crosslaminated sandy and clayey silt containing scattered stem and leaf debris. The top of this one inch-thick layer in turn was in the process of drying when the two types of dinosaurs came by and left their footprints. After this layer dried enough to become

Bed	Description	Thickness
8	Covered, sandy residuum overgrown with pines	8.5 ft
7	Sandstone, fine- to medium-grained, pale-yellowish-orange (10YR8/6) to very-pale-orange (10YR8/2), clayey and silty, con- tains scattered clayballs, fines upward	1.8
6	Siltstone, clayey, light-brownish-gray (5YR5/1), thinly laminated, contains leaf impressions (mostly conifers)	0.2
5	Sandstone, medium- to coarse-grained, pale-yellowish-orange (10YR8/6) to very-pale-orange (10YR8/2), poorly sorted, cross- bedded, base has 6 inch amplitude southeast-trending swales cut into bed below; fines upward to very fine- to fine-grained and silty	1.5 to 2.0
4	Sandstone, dominantly fine-grained but very fine- to medium, silty, yellowish-gray (5YR8/1), contains mudballs, carbon chips scat- tered on bedding surfaces, stem fragments and impressions scat- tered throughout, faintly laminated but mostly massive, symmet- rical ripples and interference ripples on laminar surfaces, dinosaur footprints within this interval	0.5 to 1.0
3	Siltstone, very fine sandy, micaceous, very pale-orange (10YR8/2), abundant leaf impressions (mostly ferns), and stem fragments, well bedded with <sup>1</sup> / <sub>8</sub> to <sup>1</sup> / <sub>4</sub> inthick impersistent laminae; some laminae contain symmetrical ripple marks; upper surface planar, anuran prints on top of this unit	2.5
2	Sandstone, fine- to medium-grained, poorly bedded, very pale-yel- lowish-brown (10YR7/2), scattered stem fragments present, pla- nar bedded with 0.5 to 2.0 inthick laminae	1.5
1	Sandstone, medium- to coarse-grained, pale-yellowish-orange (10YR8/6) to very pale-orange (10YR8/2), scattered mudballs (up to 2 in. diameter) and quartz pebbles (up to 4 in. diameter), subrounded to rounded, prominently crossbedded	10.0
Total thickness		27.0 ft

Table 1.—Section of Patuxent Formation on U.S. Route 1, 0.25 mile south of Potomac Creek.

firm, it was in turn covered by a bed of silty, poorly sorted fine- to medium-grained sand that contained abundant mudballs. This crudely graded layer ranges from 1.25 to 2.5 in. (3 to 6 cm) in thickness. The distribution of these layers appears to be quite local, as would be expected in a lower fluvial braided-stream or upper deltaic environment. There are no indications that the local environment was paludal to lacustrine, as has been surmised for much of the Arundel Formation (Glaser 1969). Although the anuran suggests proximity to permanent fresh water, the presence of well-formed footprints of any kind indicates that the local environment was damp but subaerial at the times the prints were formed. The flora of the Patuxent is strikingly similar to that of the modern warm-temperate rain forests

of New Zealand, which are dominated by broad-leafed conifers and ferns (Brenner 1963), and this implies that a similar climate existed in Virginia during deposition of the Patuxent.

Much of the Patuxent is unlithified, but some horizons in the Stafford County area are semilithified to lithified. Between 1790 and 1840, the lithified strata were quarried and used as a building stone known as "Aquia Creek sandstone" or "Virginia freestone." Parts of the White House, Capitol, Treasury Building, and National Portrait Gallery were built of this material (Withington, 1975). The strata in the footprint-bearing outcrop are only in a semilithified state, and thus unsuitable for use as building stone. Even so, their modest coherence greatly simplified collection and



Fig. 3. Stereophotos of part of an anuran trackway preserved on a counterpart slab (USNM 475487) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

preservation of the footprints described here.

Systematics.—Specimens described in this paper have been donated to the collections of the United States National Museum (USNM). Their taxonomic placement is summarized as follows:

# Class Amphibia Order Anura Gen. et sp. indet.

Two contiguous slabs (USNM 475487 and USNM 475488) from the Bachman locality preserve a single long trail of a small quadrupedal animal. The preserved impressions represent the counterpart filling of the original trackway. All but one of the tracks on one slab are shown in Fig. 3, and the entire trackway is represented in Fig. 4. Generally the tracks are poorly preserved, in part due to the small size of the animal that made them. Even so, the trackway pattern is distinctive. The animal moved with left and right rear feet spread widely apart, and it possessed front feet that appear to be notably smaller and less widely spread than the rear feet. Its gait placed left and right feet side-by-side during locomotion, rather than in the obliquely-alternating pattern that is normal for most tetrapod vertebrates during locomotion. This pattern indicates a hopping mode of progression. Although much of the trackway is indistinct, one pair of rear and front feet are fairly well preserved (Figs. 5, 6). These prints reveal the presence of three robust toes on each rear foot, with the middle toe elongated only slightly beyond the other two. The front feet are less distinct, but they appear to be elongate and rotated outward about 30° from the line of travel. As preserved, this trackway corresponds to no known animal. The relatively faint preservation of the entire trackway, however, strongly suggests that at least some of the trackmaker's toes may not have impressed into the substrate.

When our Cretaceous trackway is compared to tracks made by a modern frog (*Rana clamitans*) and a modern toad (*Bufo* woodhousei), the Cretaceous trackway can



Fig. 4. Comparison of Patuxent anuran trackway (right) with footprints made in plaster by a modern frog (*Rana clamitans*, upper left) and a modern toad (*Bufo woodhousei*, lower left). Tracks are light gray, except for *Bufo woodhousei* where light gray areas are portions of tracks that are deeply impressed and unshaded areas are portions of tracks only very lightly impressed. Dark gray area in upper right is an area of mineralization around a woody stem or branch (black). Trackway at right is shown as a set of positive prints and thus is mirror-reversed to Fig. 3. Dashed rectangle encloses footprints shown in Figs. 5 and 6. All prints drawn to same scale.

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Fig. 5. Closeup stereophotos of the third set of counterpart track fillings in the anuran trackway illustrated in Fig. 3, which is also the track set marked in Fig. 4 by the dashed rectangle.

be seen to be plausible for an anuran hopping across a substrate that was barely soft enough to record the animal's passage. Although anurans have four toes on their front feet and five toes on their rear feet, tracks made for us by modern frogs and toads hopping across wet plaster (Fig. 4) indicate that usually only the central three toes (II-IV) of the pes leave clear marks. This indicates that modern anurans primarily use pedal digits II-IV to power their hops and also implies that they use pedal digits I and V primarily for balance. Similarly, the frog only occasionally produced distinct manus prints, and the toad produced manus prints that were lightly impressed except for digit I, which was much more deeply impressed than any of the other digits. From these observations, we conclude that our Cretaceous trackway probably was made by an anuran that left only an imperfect representation of its feet. The Cretaceous anuran typically left only impressions of pedal digits II-IV, and its manus either did not leave visible marks or left impressions only of digit I. In this interpretation, the impressions of manual digit I are rotated 150° inward, which would be normal for an anuran, rather than 30° outward as would be indicated if these

marks represented the impression of the entire diminutive front foot of some very enigmatic animal.

The only characteristic of this trackway that is exceptional for an anuran is the distance between hops, which proportionally is much shorter than in modern frogs and toads (Fig. 4). Given the great antiquity of this trackway, however, there is no compelling reason to expect that its maker should have been nearly so efficient at hopping as are modern frogs or toads. Because the trackmaker maintained a steady (albeit plodding) gait, in that regard it was distinctly more like a toad than a frog. Toads can afford to be deliberate in their gait, because they possess poisonous skin glands that make them nearly immune to predation. Frogs, in contrast, must rely on their powerful hops and erratic movements to avoid attack. Therefore, the deliberate and plodding gait demonstrated by this trackway strongly suggests that its maker, although probably too ancient to be a true toad, probably possessed skin glands that produced secretions to protect it from attack. Members of the living family Discoglossidae, known as far back in the fossil record as the Jurassic, produce distasteful skin secre-



Fig. 6. Interpretation of the stereophotos of counterpart anuran footprint fillings shown in Fig. 5. Footprints are shown as counterparts for easier comparison with Fig. 5.

tions (Zweifel 1992). Therefore, it is reasonable to suggest that at least some anurans developed this type of protection by the Early Cretaceous.

Anuran trackways have not been reported in the ichnotaxonomic literature (Haubold 1971). Therefore, by definition, this trackway represents an undescribed genus and species. Unfortunately, the rather poor detail of this trackway allows diagnosis of it only to the ordinal level of taxonomy. For this reason, it is not suitable for use as a type for a new ichnotaxon. Yet even at the ordinal level of identification, this trackway is still of considerable interest. First, it is the oldest direct evidence for the existence of anurans in Virginia or anywhere else in the Eastern United States. The recent skeletal description of a functionally modern frog (Prosalirus bitis) from the Lower Jurassic of Utah (Shubin & Jenkins 1995) indicates that anurans were present in western North America well before the Early Cre-

taceous, and four living families are known to have been present by the Early Cretaceous in South America (Ascaphidae), Europe (Discoglossidae, Paleobatrachidae), and Asia (Pipidae) (Benton 1987, Carroll 1988). From these occurrences, it could be inferred that anurans were present in eastern North America in the Early Cretaceous, but none of this skeletal material provides direct proof of their presence. Second, the Patuxent specimen is attributable to an anuran specifically because of its hopping mode of locomotion. Thus, even though a hopping capability has been attributed to Prosalirus on anatomical grounds, our specimen provides the oldest direct evidence for sustained hopping locomotion in frogs.

# Class Reptilia Order Theropoda Megalosauropus sp.

Several tridactyl footprints (USNM 475489, USNM 475490, and USNM

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Fig. 7. Stereophotos of a counterpart filling of a footprint of *Megalosauropus* (USNM 475489) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.



Fig. 8. Stereophotos of a counterpart filling of a footprint of *Megalosauropus* (USNM 475490) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.



Fig. 9. A. Interpretation of footprint of *Megalosauropus* derived from the counterpart left footprint filling shown in Fig. 7. B. Interpretation of footprint of *Megalosauropus* derived from the counterpart left footprint filling shown in Fig. 8. C. Interpretation of right footprint of *Megalosauropus* (USNM 475491, not figured). D. Composite of footprint interpretations shown in Fig. 8A-C. Because the counterparts are of left feet and the positive is of a right foot, symmetries match without mirror-symmetry adjustment.

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Fig. 10. Comparison of footprint interpretation in Fig. 9A with eight genera (nine species) of theropod ichnotaxa described previously. Described footprints redrawn from Haubold (1971) and Yang and Yang (1987).

475491) are characterized by a relatively narrow divarication between digits II and IV and an elongate middle toe. These prints can be readily referred to the Theropoda. Two of these specimens (Fig. 7, Fig. 8), representing counterpart fillings of tracks, are illustrated. Both of these, as well as a third poorly preserved positive print, are interpreted by outline drawings in Fig. 9A-

C. These drawings were made by placing clear plastic film over each track, tracing its observable characteristics, and then scanning the tracings into a graphics program. The exact form of each track is different in detail, but when all of the outline drawings are superimposed at the same scale (Fig. 9D) it can be seen that they were made by feet that were identical in size and basic



Fig. 11. Stereophotos of a counterpart filling of a left footprint of *Amblydactylus* (USNM 475492) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

pattern. As all three of these footprints came from a single horizon and locality, we strongly suspect that they were all made by the same taxon of animal and quite possibly by a single individual. Thus, differences among these three tracks here are ascribed to differences in substrate and/or differences in locomotor pattern.

The fundamental foot pattern of all of these tracks clearly is that of a theropod dinosaur, and nine theropod footprint taxa have been described that either are about the same age as our tracks or show anatomical similarity to our specimens (Fig. 10). Relative toe lengths are significantly different between our specimens and *Satapliosaurus*, *Irenesauripus*, *Colombosauripus*, and *Tyrannosauropus*, so there is no reason to assign our tracks to any of these taxa. The digit divarication of our specimens differs significantly from *Jialingpus*, and the digits in *Ornithomimipus* are much less robust and more slender.

Of all of these described forms, *Huan-glongpus* and *Megalosauropus* are most similar to our specimens. Indeed, *Megalo-sauropus*, our specimens, and *Huanglong-pus* could be interpreted as merely variants of a single foot pattern on firm, moderately firm, and soft substrates respectively. As *Megalosauropus* is the earlier described taxon, and Haubold (1971) has referred

"Eubrontes" titanopelobatidus Shuler (1917) from the Glen Rose Formation of Texas to this genus, we consider it appropriate to refer our specimens to Megalosauropus. Our specimens are only about half as long as the type material of Megalosauropus (18 cm vs. 32.5 cm), and this could reflect a species level difference between our material and previously described material. However, on the basis of only three specimens, quite possibly from a single individual, it is equally possible that our specimens represent an immature individual of one of the two described species. Because our material is sparse and imperfectly preserved, we see no point in attempting a species designation at this time.

Although the foot structure indicated by *Megalosauropus* immediately suggests that it was made by a theropod dinosaur, the precise type of theropod is less readily determined. As the name implies, *Megalosauropus* initially was assumed to represent a megalosaurid or allosaurid carnosaur. But the relatively modest size of known specimens assigned to this taxon and the relatively elongate digit III are not what would be expected from the foot of a carnosaur, which should have made a footprint like *Colombosauripus*. Similarly, the foot of an ornithomimid should have made a track like *Ornithomimipus*, while the foot of a troo-



Fig. 12. Interpretation of footprint of *Amblydactylus* derived from the counterpart left footprint filling shown in Fig. 11.

dontid should have made a track like *Ire-nesauripus*. The foot of a dromaesaurid is unlike any footprint presently described in the literature. Therefore, on the basis of the foot structure of known Early Cretaceous theropods, it seems most likely that *Mega-losauropus* footprints were made by a coelurosaur or ceratosaur.

On the basis of common allometric proportions among coelurosaurs and ceratosaurs, we can determine that the animal that produced our footprints was about 9 ft (2.7 m) long and stood about 3 ft (0.9 m) high at its hips. The track maker of *Megalosauropus broomensis* was about twice this size. This range of sizes is more typical of ceratosaurs (including abelisaurids) than coelurosaurs. It is also similar to the proportions of animals, described from fragmentary osteological remains from the Arundel Formation of Maryland, that have been named Coelurus gracilis (Gilmore 1920), "Allosaurus" medius (Marsh 1888), and Creosaurus potens (Lull 1911b). Coelurus gracilis most recently has been placed in the Coelurosauria as a nomen dubium by Norman (1990). Molner (1990) has recently suggested that "Allosaurus" medius and Creosaurus potens are synonymous with each other and referred them both to Dryptosaurus, which he placed in Theropoda as incertae sedis. Any or all of these poorly known taxa conceivably could have made Megalosauropus footprints of the type described here.

# Order Ornithopoda Amblydactylus sp.

A fourth tridactyl dinosaurian footprint was recovered from the Bachman locality that can be ascribed to a different type of



Fig. 13. Comparison of footprint interpretation in Fig. 12 with nine genera of ornithischian ichnotaxa described previously. Described footprints redrawn from Haubold (1971), Currie (1989), and Yang and Yang (1987).

animal than the previously described specimens. This counterpart filling of a footprint (USNM 475492, Fig. 11, Fig. 12) is smaller in absolute size, relatively much broader, and has a relatively much shorter medial toe than that present in *Megalosauropus*. When this print is compared to other described tridactyl dinosaur footprints, all reasonable comparisons are with nine ichnotaxa of ornithopods (Fig. 13). Within this group, the great divarication of digits II and IV and the extreme shortness of digit III compare closely only to footprints assigned to the ichnogenus Amblydactylus. Digit III on our specimen is less robust than on the example of Amblydactylus shown in Fig. 13, but not all specimens presently assigned to Amblydactylus have a robust digit III (for example, see Currie 1989:297). For this reason, and also because Amblydactylus has been described previously from Lower Cretaceous strata of similar age in the western United States and Canada, we assign our specimen to that genus with some confidence. There is only one described species, *Amblydactylus gethingi*. Our specimen is unusually small for that species, so we could either have a footprint of an immature individual or a specimen referable to a new species smaller than *A. gethingi*. In the absence of any other *Amblydactylus* material from the eastern United States, however, we cannot distinguish between these two possible explanations. Therefore, it is premature to attempt any positive species assignment within *Amblydactylus* based on this single footprint.

The extremely blunt-toed appearance of Amblydactylus immediately suggests that it represents an iguanodontid ornithopod. However, the small size of our specimen is very atypical for that family, unless it represents a juvenile of a normally much larger species. If our specimen represents an adult or nearly adult animal, the track maker more probably was a hypsolophodontid, tenontosaurid, dryosaurid, or camptosaurid ornithopod. The only skeletal ornithopod material identified from the overlying Arundel Formation has been referred to Tenontosaurus sp. (Weishampel 1990). Although Tenontosaurus originally was classified as an iguanodontid (Ostrom 1970), it more recently has been referred to the Hypsilophodontidae (Dodson 1980). Its foot structure has not yet been analyzed in detail, so detailed comparison between Tenontosaurus and Amblydactylus is not yet possible. However, known Tenontosaurus skeletal material represents animals 5 to 25 ft (1.5 to 7.5 m) in length (Dodson 1980). These are all larger than the track maker at our site which, on the assumption that it was an ornithopod, was only about 3 ft (1 m) long and had a hip height of about 1 ft (0.4 m).

Summary.—Footprints from an outcrop of the Lower Cretaceous Patuxent Formation provide the first direct evidence for land animals from that unit. Three types of animals are represented: an anuran (gen. et sp. indet.), a theropod dinosaur (Megalosauropus), and an ornithopod dinosaur (Amblydactylus). The discovery of these footprints establishes for the first time that diverse kinds of terrestrial vertebrates were present in Virginia during the Cretaceous Period. Their presence suggests that the scarcity of skeletal animal remains in the Patuxent is the result of depositional or postdepositional diagenetic processes that selectively destroyed bone, and not due to any scarcity of land animals among the Early Cretaceous Patuxent landscape.

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